FEATURES OF POLLEN FLOW IN GELSEMIUM SEMPERVIRENS (LOGANIACEAE)

ROBERT ORNDUFF

GELSEMIUM SEMPERVIRENS (L.) Jaume Saint-Hilaire (Loganiaceae) is a woody vine that occurs in forested areas of the southeastern United States and of the mountains of southern Mexico and Guatemala. Its large, yellow, usually sweet-scented flowers are distylous; associated with this distyly is a strong self-incompatibility system that severely restricts intramorph and favors intermorph fertilizations (Ornduff, 1970). The flowers of *G. sempervirens* are among the largest produced by any heterostylous species and are freely visited by diverse small- and large-bodied bees, although the latter are probably largely responsible for pollination (Ornduff, 1970). The classical interpretation of distyly is that it is a morphological mechanism that promotes pollination between long-styled ("pin") and short-styled ("thrum") flowers (Darwin, 1877; and numerous subsequent workers). Recent studies of pollen flow patterns in distylous herbaceous genera such as *Lithospermum caroliniense* (J. F. Gmelin) MacM. (Boraginaceae; Levin, 1968), *Jepsonia heterandra* Eastw. (Saxifragaceae; Ornduff, 1971), *Hypericum aegypticum* L. (Hypericaceae; Ornduff, 1975), *Amsinckia* spp. (Boraginaceae; Ornduff, 1976; Ganders, 1976), *Lythrum* spp. (Lythraceae; Ornduff, 1979a), and *Primula vulgaris* L. (Primulaceae; Ornduff, 1979b) have shown that high levels of intramorph pollination also occur. In most species studied, the origin of the intramorph pollen on stigmas is unknown. It may be of intrafloral or geitonogamous origin and/or it may come from other plants of the same morph. This paper discusses pollen production, pollen removal from anthers, and features of stigmatic pollen loads in *G. sempervirens*; observations suggest that much of the intramorph pollen on its stigmas is of intrafloral origin.

MATERIALS AND METHODS

Four populations of *Gelsemium sempervirens* were studied in March and April, 1975: *8153*,[1] 10 miles south of Moncks Corner, Berkeley County, South Carolina; *8154*, 3 miles south of Cades, Williamsburg County, South Carolina; *8160*, Raleigh-Durham airport, Wake County, North Carolina; and *8161*, Globe Road near the Raleigh-Durham airport, Wake County, North Carolina. Buds and open flowers of the South Carolina plants were vapor-fixed in plastic bottles with an FAA-saturated layer of plaster of paris set into the bottom of each one. Flowers of the North Carolina plants were emasculated in the field immediately prior to anthesis, tagged, removed from the plants four days after emasculation, and, along with intact flowers also collected at the same time, preserved as above. Pollen produc-

[1] Collections from the four populations cited here were made by the author.

tion was estimated by removing anthers from buds, crushing them in 0.4 ml. 3 : 1 lactic acid : glycerol, placing a sample of the suspension on a hemacytometer, and counting the number of pollen grains on the grids. To determine the amount of pollen remaining in anthers, the same method was employed, this time using anthers of open flowers. Stigmatic pollen loads were examined by excising stigmas of open flowers, acetolyzing them, placing the centrifuged acetolyzate in lactic acid/glycerol, shaking the suspension for a standard period of time, placing a sample of the suspension on a hemacytometer, and estimating the total pollen load by counting the number of pollen grains on the grids.

RESULTS

Pollen production of pins in the two populations sampled for this trait exceeds that of thrums by a factor of 1.2 (TABLE 1). Although the average sizes of pin and thrum pollen grains are different, measurements of the two overlap to such a degree that it is impossible to discriminate consistently between the two types of pollen grains in stigmatic pollen loads. The size and composition of pollen loads on stigmas of flowers varied; in three of the four samples the total conspecific pollen load on pin stigmas was larger than that on thrums; in a fourth sample the reverse was true (TABLE 1). Foreign pollen made up from 6 to 22 percent of the stigmatic pollen loads of pins and from 4 to 16 percent of those of thrums. In population *8153*, 45 percent of the pollen produced by pins and 56 percent of that produced by thrums remained in anthers; in population *8154*, the figures were 74 and 24 percent, respectively. Pollen production figures are not available for populations *8160* and *8161*, but in both populations substantial pollen also was present in the anthers of open flowers of both forms. The stigmatic pollen loads of emasculated flowers of population *8160* were all smaller than those of intact flowers; the difference in size of the load was 68 and 64 percent for pin and thrum stigmas of this population, and 63 and 90 percent for pin and thrum stigmas of population *8161*. In three out of four samples, there were more foreign pollen grains on stigmas of emasculated flowers than on those of intact ones.

DISCUSSION

The difference between pollen production and size of the stigmatic pollen loads between pins and thrums is frequently observed in other unrelated heterostylous plants (cf. references cited above). The former is probably related to average size differences between pollen grains of the forms, while the latter may be the result of the easier accessibility of pin stigmas to visiting insects. Although large amounts of pollen remaining in anthers of open flowers is unusual, it has also been observed in the distylous *Primula vulgaris* L. (Ornduff, 1979b) and *Hedyotis caerulea* (L.) Hooker (Ornduff, unpubl.). It seems likely that in both species this results from a combination of relatively low levels of pollinator activity in very early

TABLE 1. Pollen production, composition of stigmatic pollen loads of intact and emasculated flowers, and estimates of pollen remaining in anthers of flowers of Gelsemium sempervirens.

Collection	Average pollen production per flower		Average number of pollen grains per stigma, intact flowers				Average number of pollen grains per flower, emasculated flowers				Average number of pollen grains remaining in anthers	
	PIN	THRUM	PIN		THRUM		PIN		THRUM		PIN	THRUM
			Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen	Conspecific pollen	Foreign pollen		
8153	75,511	63,966	1639	103	622	25	—	—	—	—	34,040	35,660
8154	74,059	61,172	1197	103	1861	81	—	—	—	—	54,760	14,954
8160	Not determined		1397	153	1258	139	944	333	796	102	47,260	11,677
8161	Not determined		1456	404	678	129	926	537	611	204	31,320	19,676

spring and perhaps from a feeding preference for nectar over pollen by insects visiting the flowers. The reason for large amounts of uncollected pollen in anthers of *Gelsemium sempervirens* is unclear. Bees are rather conspicuous in populations of this species when it is in flower, but no observations are available on the frequency of their visits to flowers or on other features of their foraging behavior.

The differences in the size of the conspecific pollen loads on the stigmas of intact and emasculated flowers are of particular interest. Three out of four samples of stigmas of emasculated flowers had pollen loads about one-third smaller than those of intact flowers. Since emasculated and intact flowers were both present in the same population at the same time, the total pollen available to the stigmas of the two types of flowers was the same. Consequently, the fact that stigmas of emasculated flowers of both pins and thrums have reduced pollen loads suggests that much of the pollen on the stigmas of intact flowers is of intrafloral origin. That is, a substantial proportion of pollen movement in the population is from anthers to stigmas of the same flower; clearly, any intermorph pollen on stigmas must be of interfloral origin. An alternative explanation is that emasculated flowers are less attractive to pollinators than are intact ones and are therefore visited by insects less often and/or for shorter periods of time. It is unlikely that this explanation is correct, since thrum stigmas of emasculated flowers of population *8161* received only 10 percent less pollen than those of intact flowers; the increased proportion of foreign pollen in the stigmatic pollen loads of emasculated flowers does not support reduced pollinator visitation; and the corollas have UV-absorbing and UV-reflecting zones (Eisner *et al.*, 1973), suggesting that these patterns are important in attracting insect visitors.

Thus, in *Gelsemium sempervirens* it is probable that substantial levels of intrafloral pollen transfer occur. Ganders (1974) has made a similar suggestion that in the distylous herbs *Jepsonia heterandra*, *Lithospermum caroliniense*, and *Lithospermum californicum* Gray there are moderate levels of self-pollination. Mulcahy and Caporello (1970) have arrived at like conclusions for the tristylous *Lythrum salicaria* L. I have also made a number of observations on *Hedyotis caerulea* that suggest high levels of intrafloral pollen transfer. At first glance, analyses of the composition of stigmatic loads of several heterostylous genera do not strongly support the Darwinian hypothesis concerning the adaptive significance of floral heteromorphism. However, when the interfloral component of stigmatic pollen loads can be distinguished from the intrafloral pollen, heterostyly seems to have a positive effect on intermorph pollen flow.

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DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720